What makes inventions become traditions?

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Abstract. Although anthropology was the first academic discipline to investigate cultural change, many other disciplines have made noteworthy contributions to understanding what influences the adoption of new behaviors. Drawing on a broad, interdisciplinary literature covering both humans and nonhumans, we examine (1) which features of behavioral traits make them more transmissible, (2) which individual characteristics of inventors promote copying of their inventions, (3) which characteristics of individuals make them more prone to adopting new behaviors, (4) which characteristics of dyadic relationships promote cultural transmission, (5) which properties of groups (e.g., network structures) promote transmission of traits, and (6) which characteristics of groups promote retention, rather than extinction, of cultural traits. One of anthropology's strengths is its readiness to adopt and improve theories and methods from other disciplines, integrating them into a more holistic approach; hence, we identify approaches that might be particularly useful to biological and cultural anthropologists, and knowledge gaps that should be filled.

Keywords: cultural change, innovation, cultural diffusion, social learning

Introduction

Anthropology was one of the first disciplines to subject the topic of culture to serious intellectual inquiry in regards to its nature, origin, and change over time. Early anthropologists such as Franz Boas (who was notable for his holistic four-fields approach) were concerned with documenting the wide range of behavioral variability in humans and in attributing this to cultural and historical processes rather than genetic predispositions, while acknowledging that there are some basic behavioral propensities common to all humanity (Boas 1940; Lewis 1998). Early cultural anthropologists relied primarily on the method of participant observation to document particular cultures (e.g., Malinowski 1929), followed by comparative analysis to seek patterns of between-group similarities and differences (Ember and Ember 2009). Many types of anthropologists are also interested in cultural change, i.e., in determining how patterns of behavior change within a group, or how cultural traits spread geographically (or die out) as a consequence of migration, local extinctions, shifts in political power, or changes in the environment. They integrate genetic, archaeological, historical, ethnographic, and linguistic data to answer these questions (Premo and Kuhn 2010; Steward 1955; Zhang and Mace 2021). Although anthropologists like Boas (1920) were concerned with the psychological processes by which cultural elements are borrowed from other groups and assimilated, it was rare for cultural anthropologists to closely examine the psychological processes involved in the acquisition of cultural knowledge, or to attempt to precisely model cultural evolution. With few exceptions (e.g., Durham 1991; Henrich 2017), detailed quantitative work on the mechanisms and patterns of cultural processes has been more the terrain of psychologists, biologists, sociologists, and linguists (e.g., Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981; Hoppitt and Laland 2013; Labov 2010; Tomasello 2019). **This review article seeks to highlight the most relevant work in other disciplines that informs four-fields anthropology's long-standing quest to understand patterns of cultural change.** We attempt to cite examples from both the human and nonhuman literature that represent the cutting edge methodologies. As the study of social learning has progressed over the past three decades, the methodological rigor has increased dramatically. For example, when dealing with live subjects it is no longer acceptable to call a behavior a tradition only because it increases in frequency or in number of practitioners over time. There needs to be firm evidence that the behavior spreads through social rather than asocial learning; i.e. that those individuals exposed to practitioners are more likely to adopt the behavior than are individuals that are *not* exposed to practitioners. Hoppitt and Laland (2013) review in detail the wide range of experimental and observational methods for demonstrating a role of social learning.

Cultural change involves three basic processes: invention (the creation of new behaviors), social transmission (adoption of these new behaviors by other members of the population, resulting in a "tradition"), and extinction (the abandonment of behaviors that were previously part of the behavioral repertoire). Because the topic of cultural evolution is of interest to scholars from many disciplines—including anthropologists, linguists, psychologists, biologists, and computer scientists—a variety of terms has been used for each of these processes, rendering interdisciplinary dialogue confusing. We define *invention* broadly as the creation of new behaviors and *innovation* as the spread of new behaviors (Renfrew 1978), but we note that both have been defined differently by fields with differing research goals, and some fields use entirely different terms for these concepts. For example, anthropologists and biologists frequently use the terms *innovation* to describe the creation of new behaviors (Reader and Laland 2003) and *transmission* or *diffusion* to describe a behavior's spread, whereas historical linguists use the terms *actuation* to be the "first appearance of change in a language" and *implementation* to describe the spread of this change (Trask 2000). See Perry et al. (2021) for an extended discussion of definitions (e.g., invention versus innovation).

Although human cultural psychology has some important differences from the psychology of most nonhuman species (particularly regarding dependence on symbolic behavior, cumulative cultural evolution, and active teaching), there are many commonalities in the ways that humans and other social animals invent and transmit novel behaviors. Sometimes nonhuman models are useful precisely because they are somewhat simpler in their psychology, providing insight into possible earlier stages of human cultural evolution. Humans continue to employ putatively simpler social learning mechanisms (e.g., social facilitation, social enhancement, etc.) (Kendal et al. 2018) alongside more complex mechanisms (e.g., teaching), so understanding the cultural dynamics created by simpler processes is still useful. Accurate, comprehensive data collection is often easier to achieve in nonhuman models, either because they can be studied under controlled conditions more readily than humans can, or because observational studies of nonhumans allow for more complete sampling of their behavioral repertoires and association patterns.

In this review, we summarize recent theoretical and empirical progress in identifying the mechanisms that affect the dynamics of cultural transmission at the levels of the behavior, the individual, the dyad, and the social group. We organize this review around the following six questions (Figure 1), drawing empirical examples from diverse taxa when relevant, and particularly where specific hypotheses have thus far been more rigorously tested for nonhumans than for humans. The first question asks what features of behaviors make them more likely to spread from the inventor to other group members. The next three questions ask what properties of individuals and dyads increase the probability that social learning of inventions will occur. In questions 5 and 6, we scale up to investigating the demographic and network properties of groups and populations, and ask how these characteristics affect the probabilities that behaviors will spread and be maintained, or go extinct. These questions "follow" an invention as different factors affect whether it will become entrenched as a tradition. We use this review to briefly summarize some trends in the literature, to point out some current knowledge gaps, and to suggest ways in which borrowing of methodologies from other disciplines might remedy these gaps.

The comparative method has long been used by cultural (Ember and Ember 2009) and evolutionary anthropologists (Dean et al. 2014) to study the evolution of cultural and biological traits. In this review, we make liberal use of nonhuman studies where we think the methods or results can be illuminating (e.g., of the range of factors that affect transmission). Particularly when talking about modeling studies, unless the authors state otherwise, the reader should assume that the statements made apply generally to both humans and nonhuman species, as long as those species are social animals. When the statements made are expected to apply only to a particular taxon, that will be stated in the text.

Q1. What characteristics of inventions make them more transmissible?

One early answer to this question—the notion of "cultural cores"—argued that traits or inventions spread when there is a good match between the trait and the local ecology (Steward 1955), i.e., when the benefits outweigh the costs in context. Though it might seem obvious that behaviors should diffuse only if they yield a net benefit, it is neither necessary nor sufficient that a trait be (obviously) beneficial to spread. A disabled chimpanzee learns to scratch his back with a liana, because he cannot do so with his hands; the behavior spreads to able-bodied juveniles, perfectly capable of manual scratching (Hobaiter and Byrne 2010). A human family-member produces an amusing mispronunciation ("go do good" becomes "godo gudu"); that mistake is then enshrined and repeated in a family dialect or "familect" (Gordon 2009).

We know little about what characteristics make an invention spread through a group of nonhuman animals. A rigorous answer to this question requires deep, systematic, prospective (rather than retrospective) naturalistic study of animal invention, but prospective studies are notably lacking (Perry et al. 2021). The primary prospective example (Perry et al. 2017) documented a range of novel behaviors in capuchin monkeys, including social rituals (e.g., sticking fingers deep into friends' eye sockets), foraging techniques (e.g., use of leaves to scrub irritating hairs off of *Sloanea* fruits), investigative behaviors (e.g., grooming porcupines), and self-directed behaviors (e.g., flossing of teeth with sticks or vines). Some of these behaviors spread within groups despite unclear benefits. Some of these same behaviors have been independently invented in multiple groups.

The empirical findings from capuchins suggest a link between how easily a behavior is invented and how easily it spreads. Tennie et al. (2009) propose that there is a "Zone of Latent Solutions" (ZLS), i.e., ideas or behavioral traits that typical individuals of a species could invent on their own; some of these are easy for any individual to invent and others are invented only rarely, under ideal conditions. On the ZLS account, social learning effectively helps an individual "re-invent" a behavior it could have invented on its own. Perry et al. (2017)'s findings suggest, in turn, a hypothesis consistent with ZLS: If individual A observes individual B performing a new behavior that she was *more* likely to invent herself, that behavior is more transmissible than a counterfactual, hard-to-invent behavior. This idea, though straightforward, has never been tested.

Our hypothesis —that a behavior that is easier to invent is also more transmissible —is a special case of an idea in the human literature called *content bias*, i.e, the claim that certain aspects of an invention affect its probability of transmission. Anthropologists are most likely to be familiar with the claim that folktales with "minimally counterintuitive" features are more memorable and transmissible (Norenzayan et al. 2006). Note, however, that content bias is not "purely" cognitive, as in ZLS. It is also cultural, resting on acquired notions (in the folktale example, acquired notions of common-sense).

Content bias extends far beyond the notion of "minimally counterintuitive." Studies on the spread of inventions—often called the "diffusion of innovations" —have identified *several* critical characteristics of an invention that affect transmission in humans. The most prominent inventory in humans, Rogers (2003), cites an invention or behavior's complexity, observability, trialability, and compatibility with existing ideas, social arrangements, or categories. Each of these characteristics can be teased apart into an interplay of intrinsic, cognitive, and cultural factors. A *complex* invention may have a lower probability of transmission, but complexity is relative to the recipient's cultural endowment; if an invention or new behavior is easily understood as built out of familiar parts, it is less complex than one whose building blocks must themselves be mastered (Arthur 2009; Foster 2018). How easy it is to *observe* whether others in your group have adopted an invention depends on socio-cultural context; family planning practices are much less observable if discussion of sex and reproduction are taboo. Similar arguments hold for trialability and—most obviously—compatibility.

The cultural contingency of content bias is strikingly demonstrated in the case of new technologies or scientific ideas (Fortunato et al. 2018). This literature reveals a robust relationship between the novelty of an invention and its subsequent uptake, typically discussed in terms of "impact" and quantified with proxies like citation (Fleming 2001; Foster et al. 2015; Uzzi et al. 2013). This relationship, too, is culturally contingent. Synchronously, whether an invention is perceived as novel depends on background knowledge and beliefs, which vary across scientific or technological traditions (Foster et al. 2021); this is related to the insights of sociocultural anthropologist Alfred Gell (1998) about the role played by inferences about generative processes in our reception of art and technology. Diachronously, the positive relationship between novelty and uptake is quite recent; indeed, "novelty" originally had a negative connotation, as it marked deviance from hallowed tradition. Contemporary scientists are not purely neophilic, however; inventions that add a dash of novelty to familiar material fare better, on average, than the radically new (Foster et al. 2015; Uzzi et al. 2013).

Studies of human content bias demonstrate that characteristics of inventions affect not just how transmissible they are, but *how they spread*. Consider someone who is aware of a new invention but has not yet adopted it. If their probability of adoption is constant—if it is insensitive to what other members of the population have done—then the *diffusion curve* (a plot showing the fraction of the population adopting over time) tends to follow an "r-shape" pattern, growing quickly at first and then leveling off as the susceptible population shrinks. If the probability of adoption depends on the number of prior adopters (so-called endogenous hazard), then the diffusion curve follows the famous "s-shape." Rossman (2014) has argued that these patterns are related to the *legitimacy* of the invention: whether it fits into a known and perhaps institutionalized category, or whether the category itself must spread alongside the invention. Drawing on empirical evidence from the music industry (e.g., songs that "cross over" into new radio formats or the gradual institutionalization of reggaeton music) as well as elegant simulation models, Rossman (2012, 2014) suggests that inventions from unfamiliar categories spread with an endogenous hazard, gradually switching over to constant hazard as the category becomes legitimate.

Content bias even affects the interplay between network structure and the spread of new behaviors (see Q5). The simplest models of behavior spread assume that if a naive individual has a single network neighbor who has adopted an invention, there is some chance the naive individual will adopt. This is called *simple* contagion. In a striking series of papers blending observation, experiment, and simulation, Centola and collaborators show that many important inventions spread via *complex* contagion, in which a certain number (or, in some cases, fraction) of network neighbors must adopt an invention before a naive individual will (Centola 2018). The spread of complex contagions favors dense networks; whether and why an invention follows a complex contagion depends on several social mechanisms related to its characteristics (Centola and Macy 2007), including strategic complementarity (do benefits grow with the number of adopters?), credibility, legitimacy, and emotional contagion (Collins 1993).

Many of these detailed cognitive-cultural processes are unlikely to operate in nonhuman animals, insofar as they depend on cumulative culture and institutionalization, which are believed to be rare or absent in nonhumans, though see Kamilar and Atkinson (2014) for provocative evidence of the capacity for cumulative culture in chimpanzees, i.e., nested cultural repertoires. Nevertheless, the human literature suggests the following three strategies for studying both human and nonhuman animals: First, the comparative study of many inventions and their spread *within a single species* is essential (Rossman 2014) to understanding cultural dynamics; detailed studies of single inventions give less theoretical leverage, and comparative studies are less subject to sample-selection bias that misrepresents typical patterns. Second, a combination of observational studies, formal experiments, and simulations is necessary to tease apart basic processes and determine when they operate (Centola 2018). Third, attending to the link between micro-processes of transmission and macro-patterns of adoption (at the population or network level) is often illuminating. These three strategies will help researchers clarify the extent to which human and nonhuman species differ in their cultural dynamics and the underlying cognitive processes.

The literatures on content bias discussed above lack a comprehensive framework tying together cognitive and sociocultural processes. One prominent framework that attempts to do so is cultural attraction theory (CAT). According to CAT-fanciers, transmission is *reconstructive* rather than *replicative*. The joint dynamics created by processes of production, attention, learning, and re-production produce biased directions in the space of possible behavioral traits, meaning that certain traits are more likely to emerge as stable outcomes of cultural dynamics (Claidière et al. 2014; Foster 2018). Content bias is, then, derivative of the underlying dynamics. On the CAT account, some regions of trait space (i.e., the multi-dimensional space of all behavioral traits possible for a particular species, given a set of defining characteristics or "building blocks") are attractors of the cultural evolutionary dynamics. In other words, the dynamics tend to end up in the regions that correspond to attractors. The fact that behavioral traits with particular features are widespread in a population ultimately reflects the way those features interact with (or are transformed by) proximal processes of reconstructive transmission (Acerbi et al. 2021). Our arguments above, about the importance of cultural context, reflect the fact that the dynamics for a *particular* trait are contingent on the distribution of other cultural traits in the relevant population (Foster 2018; Koch et al. 2020). Further development of a coherent, cognitively and computationally plausible theory of content bias should be a major focus in the theory of cultural evolution.

What characteristics of (Q2) models, (Q3) learners and (Q4) dyads make transmission more probable between individuals?

For a long time, it was assumed that the capacity and the propensity to use social and individual learning are a species-specific and not an individual characteristic. However, there is much evidence that the latter is the case (see Mesoudi et al. 2016). There is surely selection on individuals to have particular learning strategies that vary across the lifespan, and across learning contexts in the same life-history stage. Some individuals will be more knowledgeable and/or better models of certain behavioral traits than others, and it behooves learners to selectively observe them.

Age Theoretical models predict that for any species, younger individuals should be more open to new experiences (Sherratt and Morand-Ferron 2018). Immature individuals have the most to learn and more time to benefit from what they learn, so they are expected to spend more time seeking social information than adults. Empirical support for this prediction is found in studies of foraging in wild chimpanzees (Biro 2011) and white-faced capuchin monkeys (Barrett et al. 2017; Perry 2020). Age often correlates with experience, knowledge and skill; thus, older models generally provide more reliable information (Amlacher and

Dugatkin 2005). Because age usually covaries with size, strength, and developmental stage, a practice that works well for an older individual may not be suitable for a much younger individual who has quite different physical and cognitive abilities. In such cases, e.g., for solving difficult extractive foraging tasks, a young individual will do better to learn from a slightly older juvenile instead of a much older adult; for empirical examples from capuchins and great apes, see (Barrett et al. 2017; Russon 2003). In any species, there is likely to be an optimal age difference between learner and model, the precise value of which may vary both between and within species according to the skill being transmitted (Russon 2003) and environmental stability. Adding age structure to models of social learning yields some intriguing and counter-intuitive findings regarding when selection favors learning from older individuals vs. younger individuals (Deffner and McElreath 2020). In primates, decisions about whom to learn from seem to shift with age, starting with primary attachment figures (e.g., mother) as models in infancy, expanding the scope of possible models during the juvenile period in ways that vary according to sex and species, and changing again in the dispersing sex post-dispersal (Whiten and van de Waal 2018). Plausibly, younger individuals are not only more likely to seek social information, but also better at social learning. In some species, juveniles use different learning strategies compared to adults, and have critical developmental periods for learning certain types of things. For example, translocated juvenile turtles follow adults' travel routes to new water sources by using ultraviolet light reflective cues left by adults, rather than directly following adults; they seem to lose this learning ability in adulthood (Roth and Krochmal 2015).

Sex/gender To the extent that sexes or genders differ in their social strategies and exposures to learning opportunities, it might also be expected that members of different sexes or genders will differ in their value as models and/or will exhibit different learning strategies, and that these differences will be reflected in the patterning of social transmission. For example, vervet monkeys pay more attention to females' solutions to novel tasks (van de Waal et al. 2010), presumably because females are the non-dispersing sex, having superior knowledge of local resources. Historical linguists and sociolinguists have found that gender and age (and their interactions) are relevant to who "leads" linguistic change by rapidly adopting new variants (McCulloch 2019). Labov (1990) claims that roughly 90 percent of linguistic change is led by women, i.e., that women, relative to men, more readily adopt phonological changes introduced by more prestigious sectors of society. Subsequent work (reviewed in Sharma and Dodsworth (2020)) suggests these gender differences in propensity to lead language change are due to gender-specific types of labor that cause gender-differentiation in exposure to outside social influences.

Skill/knowledge In brown capuchin monkeys (Ottoni et al. 2005), learners paid more attention to the most efficient nutcrackers, suggesting a bias towards transmission from the more skilled individuals, but it was unclear whether the observers actually adopted these techniques. Wild white-faced capuchins appear to copy the most efficient techniques, even when invented by a peripheral, low-ranking adult male (Barrett et al. 2017). Similarly, human children prefer to copy the actions of knowledgeable models (e.g., Burdett et al. (2016)).

Rank/prestige Differences in dominance rank (roughly, intimidation-based deference), prestige (respect-based deference), or social class (socioeconomic status) may influence the probability of social transmission, especially in the short term. Prestige-biased transmission is most likely to happen in the absence of direct cues about the impact of adopting a behavior. Even when rank is unlikely to be correlated with superior knowledge, learners may preferentially copy individuals who are dominant or more prestigious (Jiménez and Mesoudi 2019; Labov 1972). In species characterized by steep dominance hierarchies in which rewards of subordinates' efforts are likely to be taken, such as rhesus macaques, low-rankers refrain from modeling useful behaviors to avoid the attention of dominants (Drea and Wallen 1999) and thus make poor transmitters. However, in species such as humans, in which there are potentially material advantages to copying and more effectively communicating with more prestigious sectors of society, prestige-bias transmission is more probable. Linguists have investigated how humans adjust their speech patterns to those of the interlocutor; sometimes it is not clear whether they are conforming as a way of being easier to understand, or to adjust their speech to more closely mirror a more prestigious conversation partner. In a study of speech patterns in New York department stores (Labov 1972), sales people (who were presumably from the same social class, which usually drops "r"s) pronounced their "r"s distinctly when talking to customers at upscale stores, but continued dropping them at bargain stores.

Personality It has long been suggested, but rarely tested, that the propensity to learn can be influenced by temperamental traits (e.g., degree of boldness or activity levels) (Dukas 1998) and that learners learn better from more tolerant models, who will allow learners to observe them at closer range (Coussi-Korbel and Fragaszy 1995). Other personality traits might also be relevant: e.g., more sociable and extroverted individuals might more readily attract the attention of learners, and thus be better "transmitters". The few empirical studies on the relationship between personality and social learning capacity show promising results: Both bolder and more anxious baboons improved at a task after they had watched a model perform the task (Carter et al. 2014), and exploratory zebra finch females were less likely to copy others in mating and foraging situations (Rosa et al. 2012). Although it seems obvious that personality is a likely influence on social transmission, operationalizing personality can be difficult. However, observer ratings of personality traits —viewed as highly suspect in the early days of animal personality research —have proven far more reliable than expected and are now widely accepted alongside more direct measures of behavioral traits obtained by scoring behaviors of individuals in either naturalistic or experimental contexts (Vazire et al. 2007).

Relationship quality The quality of the social relationship between the model and the learner is often critical to transmission success (Coussi-Korbel and Fragaszy 1995), as demonstrated in an experiment on brown capuchins (Dindo et al. 2008), a species previously believed to be incapable of imitating. The experiment showed that reliable transmission chains for solving a puzzle box could be established when using model-learner pairs with high quality relationships in which the model was dominant to, but tolerant of, the learner. Without a certain level of trust and tolerance, individuals cannot have the relaxed social interactions that permits learners to focus on details of model behavior during close-range observation of action sequences over extended periods of time. Many components of relationship quality are potentially relevant to facilitating social transmission, including the different personality types of the model and learner and the relative dominance ranks. In species with parental care (including primates), kinship is a dyadic property that is likely to influence the probability of social transmission if kin spend more time together and tolerate one another better than non-kin, but whenever possible, the relevant aspects of relationship quality should be measured via direct observations rather than using kinship as a proxy. Which aspects are most relevant could depend on the complexity of the trait to be learned: e.g., learning fine motor details of a foraging technique might require extensive close-range observation, whereas learning that a particular resource can be eaten might require quick observation from afar; see also Q1. Perry and Smolla (2020) describe a fairly general relationship quality measure, which assesses the propensity of individuals to interact affiliatively rather than agonistically; this, combined with a measure of time learners spend in proximity with models, would characterize the most relevant relationship properties in a wide range of species.

Q5. What population-level characteristics affect the degree of within- and between-group transmission?

Cultural dynamics are affected not only by individual-level processes, but also by group-level aspects like group structure and composition, which moderate how information flows across a group (Derex and Mesoudi 2020). Though each individual contributes to the cultural repertoire of the group as a whole, not all individuals have access to the entire pool of knowledge (Cantor and Whitehead 2013): Who is in contact with whom shapes who can learn what, from whom. Among others, environmental heterogeneity, homophily, and social inheritance (Cantor and Whitehead 2013; Ilany and Akçay 2016; Leu et al. 2016), can lead to nonrandom interactions among individuals (Croft et al. 2008). Social networks are a useful tool to represent and study these heterogeneous interactions. Networks are made up of two sets of elements: nodes (vertices), which represent individuals (or any other entities) and ties (edges), which represent their relationships (for a methodological introduction see Menczer et al. 2020). To describe and analyze structural features of social networks, a range of tools and metrics has been developed.

One of these measures is *network efficiency* (or communication efficiency). It is a measure of how well information can traverse a network, and is simply the inverse of the average path length, i.e., the mean smallest number of edges that connect any two vertices in the network (Latora and Marchiori 2001). At high efficiency (values close to 1), information and novel behaviors have a higher probability of reaching all group members than in lower-efficiency networks. Theory suggests that groups with efficient networks are more likely to converge on a few cultural traits, whereas groups with inefficient networks retain more cultural diversity (Smolla and Akçay 2019). Highly efficient networks can lead to cultural conservatism (a.k.a. conformity), where a group retains the same cultural repertoire across generations even if environmental incentives change. This is because, as shown in the agent-based models developed by Smolla and Akçay (2019), in tight-knit networks with low cultural diversity, novel behaviors rarely find sufficient adopters to be added to the cultural repertoire or replace an existing trait. Although these models are created with humans in mind, the logic should apply more broadly to other social taxa as well.

Cultural convergence also matters in the context of group coordination and problem-solving. The nature and complexity of the problem to be overcome determines whether quick dissemination of partial solutions or improvements through efficient networks is most beneficial to the group. Generally, groups solve problems more efficiently than individuals (Mason and Watts 2012), as long as the task is complex enough to warrant organizational efforts in allocating tasks and assembling results (Almaatouq et al. 2021). Well-connected groups find good solutions faster than sparsely connected groups (Derex and Boyd 2016; Lazer and Friedman 2007), as incremental improvements spread quickly and are adopted by most of the group. The rapid convergence onto a few solutions drastically reduces cultural diversity (Derex and Boyd 2016; Lazer and Friedman 2007; Smolla and Akçay 2019), prohibiting a more thorough exploration of the solution landscape. Groups with inefficient social networks can maintain more cultural diversity and are more likely to find globally optimal solutions, because the network-imposed restriction to information flow prevents premature adoption of one (or a few) solutions and allows concurrent exploration of different parts of the solution space (Derex and Boyd 2016; Lazer and Friedman 2007).

A second network measure with relevance for the transmission of cultural traits is the *clustering coefficient*. At the local scale, it is the probability that two nodes that are connected to a third one are also connected (i.e., the probability that a friend's friends are friends with each other). These triangular relationships are important because they have a high potential for social reinforcement. When subsets of a network are tightly connected, they are more likely to be similar in their cultural traits, which increases the probability of being frequently exposed to the same kind of information and leads to higher adoption rate of novel behaviors (Centola 2010). Clustering, like network efficiency, can lead to reduced cultural diversity (Smolla and Akçay 2019). Future research should attempt to more clearly separate the effects of the two metrics on cultural diversity.

Complex behaviors almost always build upon simpler forms that need to be acquired and mastered first. This is why acquiring complex traits often requires extended periods of learning or apprenticeship, involving extensive practice and social learning (e.g. Demps et al. 2012; Lew-Levy et al. 2017; Roux et al. 1995). Due to the sequential acquisition of traits, not every neighbor in a social network can spread traits from the group's cultural repertoire. A study by Demps et al. (2012) details information about the acquisition timing, information source, and skill level of Jenu Kuruba honey collectors: only one of the 4 skills required for honey collection could be learned in childhood, as physical maturity was required to participate in and closely observe all aspects of the process early in life. Thus, group age structure shapes learning opportunities differently for different behavior types.

While the above-mentioned characteristics similarly apply to between-group interactions, migration is specific to the between-group context (see Figure 1). Both rate of migration and the strength of conformity determine whether groups will maintain distinct cultural repertoires (Mesoudi 2018). When migrating individuals introduce novel technology that can be usefully recombined with local technology, migration can result in the production of several novel technological traits (Creanza et al. 2017). Migration can increase the number of individuals who invent and learn socially (Derex and Mesoudi 2020), and individuals in larger groups are more likely to observe and select an adaptive trait (Enquist et al. 2010; Richerson and Boyd 2020). For example, while Ache and Hadza live in small camps, they frequently migrate between camps, giving them the opportunity to observe several hundred other men making tools throughout their lifetime (Hill et al. 2014).

As the field progresses, increasingly powerful statistical techniques are developed, useful for investigating how various individual and dyadic traits are associated with the distribution of behavioral traits (Silk et al. 2018). Techniques such as network based diffusion analysis (NBDA, Hoppitt and Laland 2013) and stochastic actor-oriented models (SAOMs, Fisher et al. 2017) make it possible to model changes in networks between different points in time, using multiple co-variates. These models allow the inclusion of effects and covariates (either constant attributes such as sex or variable ones such as relationship quality) for individuals, dyads, and groups. Some problems remain with these analytical approaches: e.g., SAOMs model relationships as binary rather than continuous (i.e., either the pair has a relationship, or it does not; there is no distinction between strong and weak ties). NBDA approaches have trouble coping with a common problem in naturalistic data sets: observation gaps or undersampled periods lead to uncertainty about when individuals acquire traits, making it hard to reliably decide whether social networks are predictive of the speed with which traits are acquired.

Q6. What properties of groups make it more likely that innovations will eventually be dropped from group repertoires?

Cultural extinction (or, at least, the loss of particular cultural elements) has long fascinated historians, archaeologists, cultural anthropologists and linguists, all of whom have contributed interesting methods and theories regarding the loss of cultural diversity. Unlike the previous topics, very little is known about these processes in nonhumans. An analogy is often made between cultural transmission and genetic drift (Neiman 1995; Shennan 2001): cultural variants are lost by chance when their practitioners are not imitated before they die or leave the population. The following factors are all believed to play major roles in cultural change in humans (reviewed in Zhang and Mace 2021): dispersal, replacement of entire populations (e.g., due to conquest, epidemics, or competitive displacement), diffusion, and assimilation of one group into another. When women are captured and assimilated during warfare, culture change may be rapid, but when women engage in hypergynous marriages (as sometimes happens when ethnic groups with different subsistence types live alongside one another), the change may be slower. Frequent contact between groups enhances exchange of technologies and social innovations, leading to assimilation rather than replacement of groups.

Even in the absence of dramatic demographic change, important technological traits can be lost if the older, more knowledgeable individuals die before younger members of the society are sufficiently educated in the skills necessary to produce survival-relevant tools (see Henrich (2017) for ethnographic examples, e.g., from a Polar Inuit population). The rate of loss due to cultural drift will be higher in small populations than in larger ones, where the absolute number of experts is greater. Cross-cultural studies of fishing technologies in Oceanic populations (Kline and Boyd 2010) and nonindustrialized farming and herding societies (Collard et al. 2013) have both found that larger populations are associated with more tool types and more complex technologies (but see also Collard et al. 2005). But the connectedness of the population, and its reliance on social learning are also likely to be important: if younger members of the population are not prone to acquiring the cultural knowledge of older individuals, the products of complex cumulative culture will be lost. The importance of social learning for retention of cultural diversity was predicted in a "social learning strategies tournament", a computer-based competition that required entrants to submit a behavioral strategy that would instruct agents in a simulated world to optimally learn and exploit their environment (Rendell et al. 2011). One of the insights from the tournament was that the learning strategies that relied heavily on social learning were those most likely (by several orders of magnitude) to retain cultural variants over the long term, and to maintain a high diversity of cultural traits.

Both the number of practitioners and the frequency with which behaviors are performed are likely relevant to the maintenance of cultural traits. Social learning mechanisms such as conformity promote the maintenance of the more common behavioral traits (Mesoudi and

Lycett 2009). There is, for example, some evidence that for rare languages to survive, there needs to be a critical number of speakers of the language (Amano et al. 2014).

Between-group contact is also important for maintenance of cultural variation, allowing reintroduction of locally extinct cultural traits: contact between populations replenishes adaptive variants lost by chance, leading to higher levels of standing variation, and thus more adaptive traits (Powell et al. 2009). Between-group contact can also lead to the loss of behavioral variation. For example, eastern Australian humpback whales *Megaptera novaeangliae* adopt the songs of Western Australian populations every few years in song dialect 'revolutions,' resulting in reduced song complexity (Allen et al. 2018).

Most learners will not attain the level of expertise of their role models; these errors in social learning sometimes lead to loss of the meaning of a behavior or correct functioning of a technology, resulting in loss of the trait. This process is counteracted by the ability of individuals to learn selectively from expert practitioners: in humans, cumulative cultural adaptation occurs when unusually talented pupils surpass their teachers (Aoki et al. 2012; Henrich 2004). In larger populations, learners have access to a larger pool of experts, making such improvements more likely; thus, the equilibrium levels of cultural complexity should increase as population size increases (Mesoudi 2011).

In humans, fashion plays a special role in the study of cultural extinctions due to the rapidity with which inventions spread and go extinct. This allows researchers to observe cultural traditions from start to finish and gain insight into the psychological mechanisms involved. Both the expectation and the fact of continuous change are key elements of fashion (Cannon 1998; Davis 2013). Often new fashions appear first in the upper class and then (due to prestige bias) are copied by the middle class, only to have the elite quickly switch to new fashions as a way of differentiating themselves from the middle class (Lesure 2015).

Glossary of terms

Complex contagion: Acquisition of a novel behavior requires exposure to multiple demonstrators.

Simple contagion: Exposure to a single demonstrator suffices for the acquisition of a novel behavior.

Content bias: Aspects of an invention's 'content' that affect the probability of its transmission.

Culture: Information or behavior acquired via social learning rather than genetic transmission, that is shared by multiple members of a group.

Cultural core: The cluster of cultural traits most relevant to subsistence and economic arrangements.

Cumulative cultural evolution: Inventions are built upon over multiple social learning events, resulting in products no individual could have invented from scratch.

Diffusion: The spread of a behavior throughout a population via social learning.

Familect: A set of invented words or phrases used and understood only within a family or a similarly intimate group.

Invention: (Creation of) a behavior that is novel to an individual and their group

Innovation: Transmission of an invention to multiple individuals.

Social learning: Learning based on interaction with, or observation of, others or their products.

Social learning strategies: Context-dependent use of social or individual learning (e.g., selective observation of demonstrators with particular characteristics).

Tradition: Enduring patterns of behavior shared among members of a group that are acquired in part through social learning.

Box 1. Development and relevance of formal approaches to culture

Twentieth century evolutionary biology has seen major advances through the adoption and development of mathematically grounded theory. A similar advancement of empirical and theoretical work occurred when mathematical frameworks were adopted from population genetics and applied to cultural dynamics (Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981). Nevertheless, there remains a deeply rooted resistance against formal theoretical approaches, often due to misunderstandings of mathematical notation or distrust of the over-simplified nature of models (McElreath and Boyd 2007). There are several good reasons why so many disciplines (e.g., philosophy, economy, and physics) rely on formal theories for their deductions. Formal models replace verbal ambiguity with mathematical precision, enforcing explicitly stating assumptions. Applying these models to a range of parameters, we can test our intuition about real-world scenarios. Moreover, models can also produce unexpected emergent behaviors or counter-intuitive results that question existing understanding and provide new hypotheses for future empirical work (for examples see Servedio et al. 2014).

Recently, there have been calls to extend cultural evolution models with insights ranging from developmental psychology to cognitive neuroscience (Singh et al. 2021; Smolla et al. 2021). The aim of carefully adding complexity to existing frameworks is to better understand how previously neglected aspects of the real-world might (or might not) affect cultural dynamics. For example, effective population size—the number of individuals actually participating in knowledge transmission—can affect the number of cultural traits a group can generate and maintain (Derex and Mesoudi 2020). Commonly, theoretical models assume that any individual can acquire any cultural trait; thus, effective population size equals population size. However, from a developmental perspective, individuals may (not) be able to acquire a specific trait during particular developmental stages. This might occur when complex behaviors (e.g., mental arithmetic) build upon simpler traits that need to be acquired first, or when tasks are physically beyond an individual's abilities (e.g., tree climbing Demps et al. (2012)). For example, the theory of the zone of proximal development (Vygotsky 1978) differentiates between what an individual can learn unaided, learn with help from others, and what is currently impossible to learn. Taking this into account, effective population size would be larger for simple/easy, and smaller for complex/demanding traits. Such concepts might inspire future modeling efforts to better understand whether and how individual developmental processes impact long-term cultural dynamics.

Conclusions and Future Directions

The study of culture has expanded theoretically and methodologically. Models (both formal and simulation based) help us understand the range of what is possible, given certain assumptions, when it is impossible to collect data with the necessary time depth. Psychological studies explore the cognitive aspects of learning strategies necessary to invent and transmit behaviors. Historical and archaeological approaches, while they inevitably lack the nuance of studies on the living, provide critical insights into the past that extend the time depth of our knowledge. Studies of cultural processes in nonhuman species help us to understand which aspects of human behavioral biology are responsible for the unique form of human culture, and also permit the collection of more comprehensive naturalistic data sets than are feasible for humans; more broadly, they help us understand cultural change as an adaptive process. We are currently experiencing an explosion of new statistical methodologies that improve our ability to conduct multivariate analyses of the complex multi-level, time-varying data sets needed to see whether real-world cultural phenomena match theoretical expectations. As always, the insights of careful ethnography—the signature contribution of anthropologists—are helpful both for designing new studies and for interpreting incoming data.

Although much research has been done on how inventions become innovations and spread in populations, there are still many unanswered questions. Human inventions and inventors have been studied extensively, but little is known about what characteristics cause an invention to spread in a group of nonhuman animals. In-depth, systematic, prospective, naturalistic studies of inventions in animals are needed to answer this question thoroughly. We would greatly welcome further studies such as the one by Perry et al. (2017) in other animal species to capture the full range of animal creativity. Another important question concerns the potential relationship between the ease with which a behavior is invented and the ease with which it spreads. Comparative studies of many inventions and their diffusion are essential. This is best done with a combination of observational studies, formal experiments, and simulations or formal models; these combined approaches can decipher the underlying processes and determine when they occur. In addition to what is invented, it would also be good to know what personality traits in humans and non-humans promote invention and innovation. Particular attention should be paid to which personality traits have a positive impact on creativity and willingness to learn. Personality traits of the model should also be examined more closely, as they are crucial in determining what can be observed and to what intensity. The link between micro-processes of transmission and macro-patterns of adoption (at the population or network level) is likely to be important and worthy of investigation. At the network level, the impact of both network efficiency and clustering on cultural diversity should be explored. In modeling the networks, there are still some problems to be solved, such as how relationships are represented, how observation gaps or insufficiently captured time periods are handled, and how the spread of cultural traits affects the structure of the network. All this, of course, makes the models more complex and thus more difficult to compute and interpret. Finally, a framework linking cognitive and sociocultural processes is still lacking. The development of a coherent, cognitively and computationally plausible theory would represent an important step in the theory of cultural evolution.

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Figures

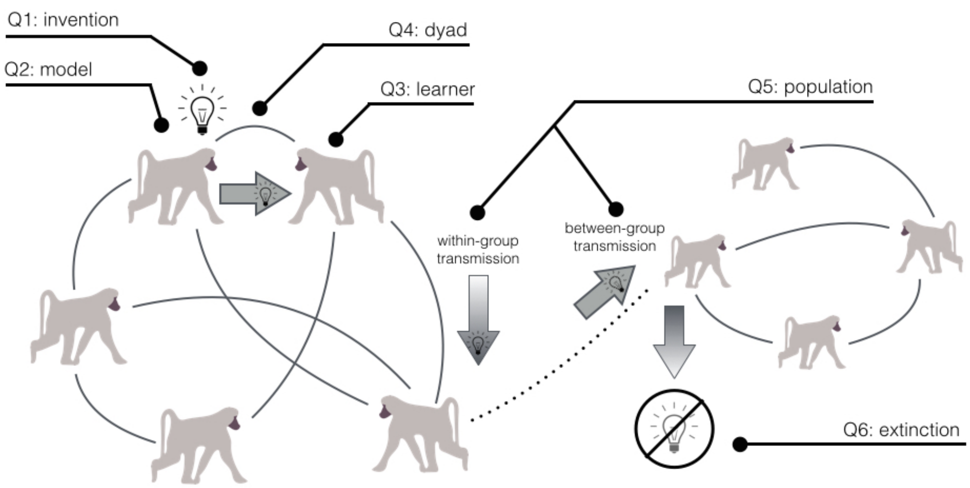

Figure 1. The creation and transmission of inventions are affected by variation at multiple levels. We review what is known about the transmission of inventions around six key questions. Some inventions, depicted here as a light bulb, are more likely to arise and spread than others (Q1). To become established as an innovation, an invention must transmit through a social group. In this figure, we depict two social groups in two social networks. Individuals in the network are depicted (arbitrarily) by cartoon baboons that can be either models or learners. Social links between individuals are depicted by thin gray lines. These links could reflect any or multiple forms of social connection, such as grooming, aggression, etc. and indicate possible paths of transmission of an invention between pairs of individuals. The transmission of an invention is indicated by the filled gray arrows with a light bulb. Graded arrows indicate the process occurring over multiple individuals within groups. The transmission between linked individuals can be affected by characteristics of the model (Q2), learner (Q3), and their relationship as a dyad (Q4). At the group level, characteristics such as group structure (depicted here by gray lines) and immigration patterns between groups (depicted by the dashed gray line), determine within- and between-group invention transmission (Q5). Finally, characteristics of some innovations result in their loss or extinction from a group or population (Q6). *Image credit: light bulb: Savio Ferreira; baboon cartoons: Ben Kawam.*